OECOPHYLLA LONGINODA, AN ANT PREDATOR OF *ANOMMA* DRIVER ANTS (HYMENOPTERA: FORMICIDAE)*

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Ants of the subgenus *Anomma,* one of 6 subgenera composing the genus *Dorylus,* are commonly referred to as "driver ants." The driver ant receives its name apparently because it "drives everything before it capable of muscular movement, so formidable is it from its numbers and bite . . ." (Savage, 1847). Of the *Dorylus* subgenera, *Anomma* is most conspicuous. Its species are aggressive, primarily epigaeic foragers (i.e. surface adapted as opposed to subterranean) with colonies consisting of up to 22 million individuals (Raignier and van Boven, 1955). Although the ferocity of the *Anomma* driver ants has been fictionalized and tales of their behavior are incorporated into African folklore, their pugnacity has been repeatedly documented (Loveridge, 1922; Raignier and van Boven, 1955; Savage, 1847, 1849; Wheeler 1910, 1922). The driver ants have also been described as clearly dominant animals (Weber, 1943). Without a doubt, they appear as efficient predators, having evolved a system of group predation of significant adaptive advantage in tropical environments.

However, these carnivores are themselves not without predators. Bequaert (1922) reports *Anomma* species from the stomachs of 4 species of African toads (genus *Bufo*) and 3 species of African frogs (in the genera *Rana, Kassina, Hemisus*). He also reports that driver ants are commonly eaten by African skinks of the genus *Mabuya* and by pangolins (scaly anteaters) of the genus *Manis.* Chapin (1932) indicates that driver ants are eaten by several species of African birds, including the Guinea fowl, *Phasidus niger* Cassin. My own observations in Ghana place the domestic chicken among *Anomma* predators, for driver ants frequently forage in village refuse heaps where chickens are also regular visitors. These chickens walk along the columns and clusters of worker ants, picking up and swallowing individual workers while carefully avoiding any other contact with the ants. Insects and other arthropods have not been observed as important *Anomma* predators. While flies of the genera

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Bengalia (Calliphoridae) and *Stylogaster* (Conopidae) are recorded as *Anomma* predators (Cohic, 1948), the term predator is applicable only in the case of *Bengalia*. *Bengalia* flies fly about and land near *Anomma* columns and eventually dart toward individual workers, stealing their prey or brood (Bequaert, 1922). *Stylogaster*, on the other hand, is parasitic on insects, particularly cockroaches, that flee before *Anomma* foraging swarms, and on tachinid and muscid flies that are attracted to such swarms (Smith, 1967). *Stylogaster* is also abundant over the swarms of New World dorylines, and parasitizes cockroaches and tachinid flies (Rettenmeyer, 1961). The eggs of these conopids are inserted into the host cuticle, and the larvae are internal parasites.

During May and June of 1971, while collecting driver ants in Ghana, I observed on 5 separate occasions the ant *Oecophylla longinoda* (Latreille) (subfamily Formicinae) successfully attacking *Anomma* workers. It became apparent that *O. longinoda* is a common predator of driver ants and that it may be one of the very few insect predators of the subgenus.

Two other species of ants were seen to attack *Anomma*, but each case involved unusual circumstances. In the first case, workers of the ponerine ant *Paltothyreus tarsatus* (Fabricius) carried off the larvae and pupae of *D. (Anomma) nigricans* Illiger that had been discarded while the nest of the *Anomma* colony was being excavated. In the second case, a small species of *Crematogaster* dragged away *Anomma* workers that had been injured by an automobile that passed over an *Anomma* column. (Note: driver ants move in columns, usually along well marked trails, during foraging and during emigration or nest relocation). Cohic (1948) also records an encounter between *Crematogaster* and *Anomma*.

O. longinoda, commonly referred to as the red tree ant, is concentrated in several areas in the Ethiopian Region and is considered to be an efficient predator with a painful bite (Vanderplank, 1960). This ant is dimorphic, with its maxima caste performing the foraging tasks (Weber, 1949). Although *O. longinoda* previously has been recorded as a predator of *Anomma* by Cohic (1948), Ledoux (1950), Vanderplank (1960), Way (1954), and Weber (1949), the extent of this predation was, in most cases, not indicated. Note: the major weapons in predatory attack for both *Oecophylla* and *Anomma* are the mandibles. *O. longinoda*, a formicine ant, is stingless, while *Anomma* workers possess what appears to be a functionless sting.

Of the 5 observations of *Oecophylla* predatory behavior, 2 occurred in the coastal scrub and grassland region at Legon and 3 in the moist semi-deciduous forest region (2 at Kade and 1 at Tafo), and each involved predation on the species *Anomma nigricans*. Although all African populations of *Oecophylla* are considered to be one species, the observations at Kade involved the commonly occurring dark form.

Discussion

O. longinoda attacks both emigrating and foraging columns of *Anomma*, but attacks the columns at a limited number of selected points. In some cases the *Anomma* trails over which the columns move are marked by soil particle walls, while in other cases, the columns march along completely exposed trails or trails covered in part by grasses and organic debris. Some trails are subterranean or covered with soil particle ceilings built by the *Anomma* workers. In the observations reported here, the *Anomma* trails either had soil particle walls or were partially covered by organic debris (primarily leaves).

Single *Anomma* workers are removed from the column by individual foraging *O. longinoda* workers. The *O. longinoda* workers are either positioned outside of the soil particle walls or on leaves and twigs adjacent to or overhanging the *Anomma* column. An *O. longinoda* worker quickly thrusts its head into the column, grasps an *Anomma* worker in its mandibles and pulls it from the moving column. In one case (Tafo) the *O. longinoda* workers removed *Anomma* workers from a diffuse column expansion. The *Anomma* workers are rarely alarmed by the removal of a single sister worker, although in one instance, the *O. longinoda* attack was so widespread that the *Anomma* column was subsequently disrupted. *O. longinoda* workers are obviously afforded some protection by the trail wall or by the space between the column and their position on the surrounding vegetation (Fig. 1). *Anomma* workers are generally excitable and easily disturbed, and thus it is surprising that they are usually so little disturbed during an *Oecophylla* attack.

Way (1954) notes that *O. longinoda* grabbed *A. nigricans* workers from the column, but adds that the *Anomma* workers had "strayed from the main stream." While it is true that the *Anomma* workers selected by *O. longinoda* foragers are peripherally located in the column, they are not usually "strays." Way (1954) also reports that *Anomma* soldiers were never taken, but I observed on several occasions soldiers being attacked and immobilized. Although most *Anomma* workers attacked were not of the soldier caste, this may

Fig. 1. Captive *Anomma* worker (indicated by arrow) and attacking *O. longinoda* foragers at the beginning of the immobilization phase of predatory attack.

be merely a reflection of the polymorphic proportions of the colony population.

While the removal of *Anomma* workers from the column is performed by individual *O. longinoda* workers, the immobilization of prey is the result of group action. *O. longinoda* workers surround the initial foraging worker and its *Anomma* captive and bite and grasp the *Anomma* worker extremities, and at the same time begin pulling (Fig. 1). Additional *O. longinoda* workers are recruited to this task, perhaps by the secretion of alarm substances. The mandibles, legs, antennae and parts of the alitrunk, petiole, and gaster are grasped (Fig. 1). Anywhere from 5 to 20 *O. longinoda* workers arrange themselves around the *Anomma* worker. In all cases, regardless of *Anomma* worker size, captured workers were incapable of mounting an adequate defense and were unable to bite their captors (i.e. they are unable to reach the *O. longinoda* worker because of their position in its mandibles).

The *Anomma* worker is immobilized through prolonged stretching, and this method of prey immobilization is common in *Oecophylla* (Gressitt, 1956; Ledoux, 1950; Vanderplank, 1960; Way, 1954; Weber, 1949). The stretching of prey, spread-eagle fashion, may be common to predaceous ants whose mandibles, perhaps in combination with their stings, are not efficacious, at least at the individual level, in quickly killing or immobilizing prey. For instance, New World doryline swarm raiders, such as *Eciton burchelli* (Westwood) and *Labidus coecus* (Latreille) stretch their large prey until it is torn to pieces (Schneirla, 1971). In this case, not only does the stretching serve to kill the prey but to subdivide it as well, thus facilitating the transport of the prey back to the bivouac. The *O. longinoda* mandibles do not appear to pierce the integument of the *Anomma* workers, although Way (1954) notes that the soft cuticle of limb and abdominal joints of prey is sometimes breached. He further reports that the *O. longinoda* workers sometimes curl their gasters dorsally and spray "poison" on these wounds.

After the *Anomma* worker is immobilized, it is usually carried by one or two *Oecophylla* workers to their arboreal nest. If the *Anomma* worker is not completely immobilized, more than 2 workers may cooperate in carrying it to the nest. In one observation, the *Anomma* worker was pulled at and stretched for 20 minutes, resulting in almost complete immobilization. Four *O. longinoda* workers then proceeded to carry the worker up a tree trunk, 1 grasping the *Anomma* mandible, 1 an antenna and 1 each the metathoracic legs. The *Anomma* worker occasionally moved its legs, catching its tarsal claws on lichens and mosses growing on the bark. Eventually 2 workers managed to carry it up into the tree. Way (1954) timed the stretching of a honeybee by *O. longinoda* workers and found it also lasted 20 minutes.

The predatory attack of *O. longinoda* on *Anomma* driver ants is thus divisible into 3 phases: (1) the attack phase, in which an individual *Anomma* worker is seized and removed from the column; (2) the immobilization phase, in which additional *O. longinoda* workers are recruited to stretch the *Anomma* worker until it is no longer able to move; and (3) the transfer phase, in which the immobilized *Anomma* worker is carried to the *Oecophylla* nest.

Although in all observations the *Oecophylla* workers carried off many *Anomma* workers, the number may not be significant with respect to the total number of *Anomma* workers comprising a colony. Way (1954) notes, in his observations of *Oecophylla* attacks on *A. nigricans*, that in one case, in a period of an hour, 348 *Anomma* were carried into one tree and 252 into another.

The importance of driver ants in the diet of *O. longinoda* cannot be calculated at this point. It is known that insect prey and sugars are essential for the survival and reproduction of an *O. longinoda* colony (Vanderplank, 1960). The role of *Anomma* as a food source may depend, to a large extent, on chance movements of *Anomma* columns into *Oecophylla* colony territories. Obviously the probability of such an occurrence depends, in part, on the colony densities of prey and predator in a given area. The efficiency of foraging behavior in *Anomma* may in itself increase the probability of chance encounters with *Oecophylla*. Numerous foraging columns, for instance, may simultaneously work out from an *Anomma* nest, may frequently change direction, and may start anew each day, thus enabling the colony, in its search for nutrient sources, to probe the environment in many directions.

Are the roles of predator and prey in the *Oecophylla-Anomma* interaction ever reversed? Evidence for such a reversal might be found in the prey materials carried by *Anomma* workers back to the nest. I made 11 extensive surveys of prey taken from *Anomma* foraging columns in areas where *O. longinoda* is also found, and in only one sample was there such evidence. It contained the gaster of an adult *O. longinoda* worker. It appears that *O. longinoda* is not often attacked by *Anomma*, though it is not likely that *Oecophylla* could effectively resist an *Anomma* foraging swarm. However, it is probable that the arboreal nests of *O. longinoda* are simply out of reach of *Anomma* foragers. My own observations indicate that while

Anomma does forage in trees at heights greater than 10 feet, they are less likely to do so than they are to forage in lower vegetation. Cohic (1948) reports that while he observed *D. (Anomma) nigricans* foraging in trees to heights of about 10 meters, the nests of *Crematogaster* and *Oecophylla* were spared or avoided.

Summary

1. *O. longinoda* is an important predator of *Anomma* driver ants and may be the single most important insect predator of *Anomma* in areas where the two are sympatric.
2. In attacking *Anomma*, an *O. longinoda* worker reaches into a moving *Anomma* column (foraging or emigrating) and seizes an individual *Anomma* worker in its mandibles, pulling it quickly from the column. This is termed the attack phase of the predatory interaction.
3. After the *Anomma* worker is removed from the column, the initial *O. longinoda* forager is joined by sister workers, which together immobilize the prey through prolonged stretching. This is termed the immobilization phase.
4. When the *Anomma* worker is sufficiently immobilized, it is carried back to the *Oecophylla* nest by 1 or more workers. This is termed the transfer phase.
5. Individual *Anomma* workers are unable to successfully defend themselves, and little or no alarm is generated in the column when the worker is removed.
6. All *Anomma* workers, regardless of size, including soldiers, are subject to *O. longinoda* attack.
7. Immobilization of prey through prolonged stretching may be employed by predaceous ants whose mandibles and/or stings are ineffective in subduing prey at the individual level.
8. *O. longinoda* is an effective predator of *Anomma* because, (a) it usually attacks the *Anomma* column at a limited number of points and generally avoids disrupting *Anomma* movement; (b) it seizes and removes *Anomma* workers from the column quickly, thus avoiding a widespread alarm response; (c) it attacks from defensively advantageous positions outside of the column, reducing its vulnerability to *Anomma* alarm response.
9. In areas densely populated by *O. longinoda* (where the probability of chance encounter is high), an *Anomma* colony may lose several hundreds, theoretically thousands, of workers per day to *Oecophylla* predation.

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